Animal Behaviour 79 (2010) e18–e23

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Final response: sexual selection needs an alternative

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ARTICLE INFO

Article history:
Received 20 November 2009
Initial acceptance 30 November 2009
Final acceptance 14 December 2009
Available online 27 January 2010
MS. number: 09-00740

Keywords:
behavioural ecology
competition
density dependence
game theory
genial gene
mating systems theory
Nash bargaining solution
selfish gene
sexual selection
social selection

Shuker (2010) enumerates five points and we organize our response accordingly.

First, we agree that sexual selection (and social selection) are subsets of natural selection, and therefore share the same logical framework of natural selection. We do not agree that natural selection is ‘driven by competition, be it competition for resources or competition to avoid death, as ultimately something limits population growth’. It is true that in Chapter 3 of *The Origin of Species*, Darwin (1859) wrote of natural selection as a struggle for existence caused by resource limitation, as ‘the doctrine of Malthus applied with manifold force to the whole animal and vegetable kingdoms’ (page 63), and wrote, ‘There is no exception to the rule that every organic being naturally increases at so high a rate, that if not destroyed, the earth would soon be covered by the progeny of a single pair’ (page 64). This framing of natural selection as resulting from resource competition was superseded by the neo-Darwinian formulation of early population genetics in which fitness is understood as the product of fertility with survival. Conferring a higher fitness by this definition is sufficient for a gene to fix in the gene pool without reference to competition for resources. A higher fitness could be attained with higher efficiency under unlimited resources.

To say that natural selection is always driven by competition widens the meaning of competition beyond common usage in ecology. For example, the colonization phase of community succession, which lacks competition, is distinguished from the climax phase in which competition occurs. Similarly, the r-selection phase of population dynamics during density-dependent evolution involves natural selection for efficiency and productivity whereas the K-selection phase involves natural selection resulting from competition. To be sure, evolutionary writers sometimes view *all* natural selection as resulting from competition regardless of whether resources are limiting. Bell (2008, p. 15), for example, refers to ‘competition’ as occurring when ‘variants with greater exponential growth rates are selected’ during density-independent population growth (i.e. during r-selection), saying that ‘the nature of competition changes’ when the population dynamics transition from density-independent selection to density-dependent selection (i.e. from r-selection to K-selection). We do not consider r-selection, that is, differential density-independent growth, as

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doi:10.1016/j.anbehav.2009.12.029

'competition'. If competition and natural selection are synonymized, saying that competition 'drives' natural selection is empirically meaningless because this is then true by definition and could not be falsified, and moreover imparts the ideological connotation that competition enjoys a logical priority and universality in biological evolution. Instead, competition for resources, that is, crowding in the original Darwinian and Malthusian sense, is merely one of many mechanisms that can cause natural selection, and it is not always present. Even though natural selection is indeed ubiquitous, it does not follow that competition is ubiquitous too, and in particular, it does not follow that competition for mates is ubiquitous either.

Second, we agree that what Shuker terms 'mating systems theory' is not the same as sexual selection itself. We recognize a distinction between core and peripheral issues pertaining to sexual selection by referring to a 'central narrative' within the sexual selection 'system' of theories. Our terminology draws attention to the logical connections among these theories. Mating systems theories expand upon the sexual selection narrative and sexual selection theory relies on mating systems theory to make concrete predictions. Take, for example, extrapair copulation (EPC). By any definition of core sexual selection, the explanation of EPCs lies beyond the core. If one views the core of sexual selection as being about females selecting males for good genes, then EPCs follow logically as a tactic for females to secure a genetic upgrade over their pair male. So, failure to confirm that extrapair males have better genes than pair males reflects back on the truth of core sexual selection that was the premise from which this particular EPC theory was derived. Such a failure to confirm would at least provoke a restatement of what can be derived from the core specifically concerning EPC, and if many such theories were found to be unconfirmed, a reexamination of the truth of core sexual selection. The point is, any definition of core sexual selection is logically connected to the peripheral theories pertaining to it, including all of mating systems theory as well as many other issues such as the evolution of anisogamy (cf. Roughgarden 2009, Table 19, pp. 237–238), all of which unite as one of evolutionary biology's master narratives. Thus, sexual selection and mating systems theory are logically interdependent, and falsifying either of these components within the sexual selection system has repercussions for the other components.

Shuker defines core sexual selection as 'the selection of traits associated with competition for mates'. Moreover, he defines a mate as 'a reproductive partner with which one or more zygotes are formed' thereby ruling out the ample variety of known same-sex matings, even though same-sex matings might carry out the same social functions as between-sex matings. This definition allows that much sexual activity, both hetero- and homosexual is not about mating, and is not part of mating systems theory, but of some other topic, such as the emerging subject area of animal friendships. Moreover, as stated, Shuker's definition refers solely to behaviour. However, Shuker also requires that the traits involved must be heritable, and Shuker describes 'sexual selection as a component of an overall natural selection process, and inclusive of both selection and heredity'. We agree that sexual selection pertains to behaviour with evolutionary consequence, and not to the behavioural act of mate selection itself.

Shuker considers that his definition of sexual selection 'represents the consensus among evolutionary biologists of what sexual selection is'. We think this perception of consensus requires careful picking of the sample population. In our experience, most biologists, including evolutionary biologists, together with present and former biology students, not to mention social scientists such as evolutionary psychologists and anthropologists, think of a specific narrative when queried about what sexual selection is. They think of males fighting with one another for access to and/or control of females, of females choosing males whose good genes are revealed though displays, ornaments or armaments, and of an evolutionary rationale for such behaviours that traces to sperm being cheap and eggs expensive. Most biologists are then surprised to hear that this archetypal narrative may often be incorrect, and they are especially surprised when an archetypal example such as the peacock needs reinterpretation. Shuker relegates this archetypal sexual selection narrative to the domain of 'mating systems theory', many parts of which Shuker allows 'could be wrong' and which he also acknowledges show a 'lack of experimental work'. He states further that, 'clearly our grasp of mating systems is not as complete as we perhaps thought'. But relocating the archetypal narrative of sexual selection to mating systems theory so that its failure can be dismissed as having 'no effect at all on the logical basis of sexual selection' is evasive, or as Shuker himself recognizes, very 'convenient'. If one is serious about placing mating systems theory, including the archetypal narrative of sexual selection, at arms length from 'core' sexual selection, then textbook writers and other decision makers who influence biology curricula worldwide should be informed so that the present widely taught accounts of sexual selection can be revised.

We do not feel strongly about how sexual selection is defined, provided that the definition allows sexual selection to be falsified with data and acknowledges that alternatives exist. We object when the definition is slippery, infinitely malleable, and continually revised in light of contrary data, making the theory unfalsifiable. In our own work, we typically employ a definition of the 'central narrative' that is closer to Darwin's original statement than is Shuker's definition, namely, that sexual selection is 'Natural selection from differences in mating success. Males compete for mating opportunities, females are a 'limiting resource' for males, and females choose males for genes' (Roughgarden, 2009, Table 1, page 62). We argue that sexual selection in this sense does not occur, and we accept Shuker's observation that 'the criticisms of Roughgarden and colleagues lead more to mating systems theory than they do to sexual selection per se', according to his definition. In this light, the reservations Shuker has expressed about the correctness of present-day mating systems theory are an important concession. Still, for the present exchange we are happy to work with Shuker's broad definition of sexual selection, namely, as any selection resulting from competition for mates, which we do accept as concrete and falsifiable. However, by this definition too, the evidence for sexual selection is weak, as discussed further in point five below.

Third, we disagree with the claim that 'the action of sexual selection is unaffected by whether the behavioural interactions between mating partners during reproductive episodes are considered cooperative or selfish'. By the letter of Shuker's own definition of sexual selection, namely selection associated with competition for mates, if the interactions between potential or actual mates are anything other than competitive, say cooperative, then manifestly, sexual selection is not taking place.

Still, the text of Shuker's comment dwells on what he feels is the importance of competitive game theory in behavioural ecology and the sufficiency of Maynard Smith's (1982) evolutionarily stable strategy (ESS) concept in particular. He also remarks that our alternative modelling framework pertains to 'the evolution of parental care, not sexual selection at all', and as such is banished to the hinterland of mating systems theory.

We suspect the discussion here is at crossed purposes. Our position is that sexual selection theory misconceptualizes the reproductive process. Sexual selection focuses entirely on mating, both the act of mating and the identity of the mating partner, and relegates what happens next to a distinct topic of 'parental care'.